DEVONIAN FISH AND PLANTS FROM THE BOKKEVELD SERIES OF SOUTH AFRICA

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ABSTRACT

Fossil fish and plants from upper strata of the Bokkeveld Series of Barrydale, Cape Province, Republic of South Africa, are described. The fishes are represented by arthrodire placoderms, *Barrydalaspis theroni* gen. et sp. nov., a phlyctaenaspid arthrodire and, possibly, *Groenlandaspis*; an acanthodian spine indistinguishable from *Gyracanthides warreni* White; and an egg case. The plants are represented by lycopods: *Archaeosigillaria plumsteadiae* sp. nov., *A.* cf. *picosensis* Kräusel & Dolianiti, and two different types of lycopod endocortical cast. The fishes and plants are compared with those in Australia, Antarctica, North America and South America, and it is concluded that these Bokkeveld fossils are either Middle or Upper Devonian.

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INTRODUCTION

In 1974 a small collection of fossil fish and plants was sent to one of the authors (B. G.) for identification by Dr J. N. Theron of the Geological Survey of South Africa. The material comes from the upper strata of the Bokkeveld Beds at Barrydale, Cape Province, Republic of South Africa. Precise locality information is not available.

The Bokkeveld Series is reputed to be of Devonian age (Du Toit 1939) and therefore the presence of fish is of significance because, with one possible exception, fish have not previously been recorded from the Devonian of South Africa. This one possible exception is a reference to the occurrence of *Machaeracanthus* in the Bokkeveld Beds which is given without detail by Du Toit (1939: 222). It is possible that Du Toit extracted this record from Schwarz (1900) who referred to a fossil fish spine. At the very best, therefore, Devonian fish from southern Africa are very poorly known and this collection adds a new dimension to our rapidly increasing knowledge of Devonian fish from the Southern hemisphere.

The primary purpose of this paper is to describe these fishes. The fish are associated with a few plant remains and these are described and discussed (W. G. C. & A. J. H.). A few notes are added concerning the age of the Bokkeveld Beds based on comparisons of the fish and plants with those preserved in presumed contemporaneous strata in North and South America, Antarctica, Australia and west Africa.

The fish are represented mainly by placoderms, but an acanthodian and the impression of a large egg case are also present. This last is particularly interesting since the form of the egg case is similar to those attributed to chimaeroids which are not known prior to the Jurassic. The plants are represented by several types of lycopods. All the fossils are poorly preserved, the majority being represented as impression or internal casts. The matrix is a texturally variable and poorly bedded micaceous siltstone. Because of this and the type and condition of the contained fossils, it appears as if the sediment was deposited in a freshwater environment and that the fossils lived in the place of sedimentation.

The specimens referred to in this paper come from the collections of the South African Museum, Cape Town and from the Geological Survey, Cape Office. The former are prefixed by SAM; the latter are left unprefixed, simply being quoted by the field number.

THE FISH REMAINS

ARTHRODIRES

A number of facts have made the study of the arthrodires difficult; only impressions of the plates remain; with few exceptions the plates are isolated and sometimes broken, making it difficult to associate parts of animals; there is some degree of post-mortem deformation with resulting distortion. Nevertheless, the margins of the plates are perfectly angular, ruling out the possibility of post-mortem/pre-depositional transportation. Among the specimens several show associated ventral thoracic armour and on the basis of these two types of arthrodire can be recognized. Some isolated plates of the lateral aspect of the trunk shield can be referred to one or other of these types. It has been decided to name one of these because it is distinctive from other named arthrodires. The second arthrodire type shows a general similarity to named arthrodires from elsewhere. To avoid cluttering the already burdensome literature with yet another name, this is referred to as a 'phlyctaenaspid arthrodire' with the implication that what little is known of this form is similar to *Neophlyctaenius* and presumed close relatives. Additionally, specimens of a head and a piece of a large arthrodire are briefly mentioned.

Order ARTHRODIRA

Suborder PHLYCTAENIOIDEI Miles 1973

Infraorder and Family incertae sedis

Genus ***Barrydalaspis*** gen. nov.

(Figs 1–4, 6A)

Etymology

From Barrydale, South Africa, the area in which these fossils are found.

Diagnosis

Phlyctaenioid with short, broad ventral thoracic armour; spinal long with denticles along the medial edge, spinals set at a very divergent angle; subpectoral emargination broad; interolateral with prominent transverse groove; anterior ventrolateral of either side meeting its partner in the mid-line; anterior dorsolateral with a prominent groove on the lateral face of the anteroventral corner; ornament consisting of small, simple tubercles; body behind thoracic shield at least partially covered with scales.

Type species

Barrydalaspis theroni sp. nov.

Barrydalaspis theroni sp. nov.

Etymology

Named after Dr J. N. Theron who brought this material to the attention of the authors.

Holotype

SAM–K4647, the impression of the ventral thoracic armour from the Bokkeveld Series of Barrydale, Cape Province, South Africa.

Other material

SAM–K4648–50, K4770–73, K4766, K4779, K4785, K4789, K4791, and an anterior dorsolateral plate preserved on K4798.

Diagnosis

As for genus, only species.

Remarks

The ventral thoracic armour shows a superficial resemblance to that of the petalichthyid *Lunaspis* (see Gross 1961); the armour is short and broad and the spinals are set at a divergent angle. However, unlike *Lunaspis*, *Barrydalaspis* shows well-differentiated posterior ventrolaterals. (Gross (1961) describes two pairs of plates lying behind the anterior ventrolaterals in *Lunaspis*, the posterior ventrolaterals and the postero-ventrals. These are interpreted as body scales by Miles & Young (1977) and their interpretation is accepted here.) Furthermore, the dorsal part of the armour is similar to that of a phlyctaenioid and unlike that of a petalichthyid in showing a 'ball and socket' dermal neck joint and a large posterior dorsolateral.

The anterior ventrolateral (AVL) is short and broad, being 1,35 times as wide as long in the smallest individuals and 1,25 times as wide as long in the

Fig. 1. *Barrydalaspis theroni* gen. et sp. nov. Silicone cast of holotype showing ventral thoracic armour in external view.

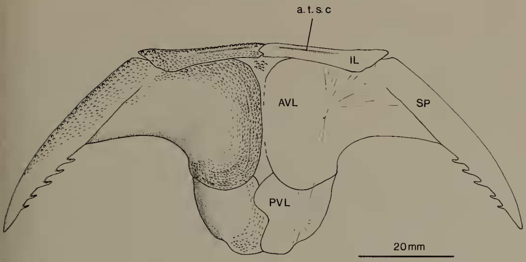

Fig. 2. *Barrydalaspis theroni* gen. et sp. nov. Restoration of the ventral thoracic armour in ventral view. Based on SAM–K4647 and K4649. AVL—anterior ventrolateral, IL—interolateral, PVL—posterior ventrolateral, SP—spinal, a.t.s.c—anterior transverse sulcus.

larger (presumably older) individuals. With this change in linear dimensions there is also a change in shape, the posterior area of the AVL becoming squarer with increasing size (cf. Figs 1 and 2). The length of the spinal margin, expressed as a percentage of the maximum width of the plate, also varies from 48 per cent in the small individuals to 44 per cent in the large specimens. A similar decrease in the relative length of the spinal margin has been recorded for *Coccosteus* by Miles & Westoll (1968: 433–434). There is a well-marked 'Ventrolateralkante' (Gross 1933) running longitudinally on the posterior part of the AVL and across the posterior ventrolateral. This implies that there was a narrow subpectoral wall of the flank armour and the development of a postbrachial lamina. The centre of radiation of the AVL lies remarkably far forwards, more so than in any of the 'dolichothoracid' types figured by Denison (1958, fig. 112). The ornament on the AVL consists of simple tubercles which are very small at the radiation centre but become larger along the anterior, median and posterior margins. Ornament is absent from that part of the plate adjacent to the subpectoral emargination. A similar lack of ornament is noted by Miles & Westoll (1968) in the corresponding area of *Coccosteus*.

The visceral surface of the AVL shows that perichondral bone lined the scapulocoracoid. Impressions left by this perichondral layer suggest that the abdominal division and the coracoid process of the scapulocoracoid (terminology of Stensiö 1959) were both very broad, as in most 'dolichothoracids'. In some specimens the contact faces with the anterolateral can be seen, suggesting that the width of the pectoral fenestra is equal to about half the length of the subpectoral emargination.

The posterior ventrolateral (PVL) is a little longer than broad and, as usual, the left PVL overlaps the right. As mentioned above, there is a strongly

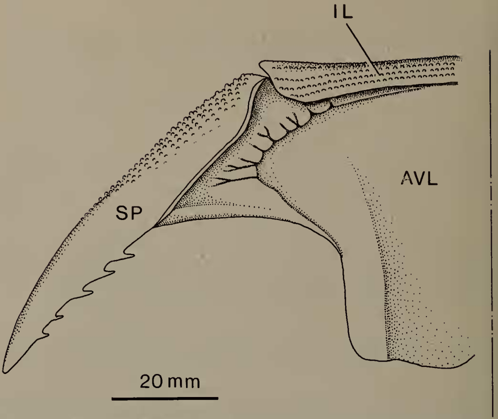

Fig. 3. *Barrydalaspis theroni* gen. et sp. nov. Restoration of anterior ventrolateral, interolateral and spinal of the left side in visceral view. Based on SAM–K4779, K4770, K4791 and K4771. Abbreviations as in Fig. 1.

developed 'Ventrolateralkante' which divides the plate into lateral (vertical) and ventral (horizontal) laminae. The lateral lamina, which is relatively long, suggests that the postbrachial lamina was also long, as in phlyctaenaspids (Denison 1958: 534). The ornament is similar to that on the AVL. The medial margin of the left PVL is 'S'-shaped where it overlaps the right but there is no indication of the complex overlap relations seen in *Tiaraspis* and *Romundina.*

The spinal (SP) is relatively long and the proportions agree more with those of Denison's phlyctaenaspid genera than with those of any other arthrodire group. The spinals are relatively longer in smaller individuals. A suture between the SP and AVL can be traced except anteriorly. As mentioned in the diagnosis, the SP is set at a very divergent angle, this being approximately 50°. *Phlyctaenius acadica* also shows a spinal set at a high angle (about 48° from the restoration given by Heintz 1934), but in this species the SP is much shorter. The ornament consists of well-developed tubercles along the lateral edge of the anterior two-thirds. Smaller tubercles are also present over half of the ventral surface and about one-fifth of the dorsal surface. Posteriorly, the medial edge bears six to eight recurved denticles.

The interolateral (IL) is orientated almost transversely and has ventral (external) and dorsal (internal or postbrachial) laminae which both become wider laterally. On the ventral lamina there is a shallow sulcus between two rows of tubercles. This sulcus, which has been variously named in arthrodires ('anterior ventral sulcus'—Miles & Westoll 1968; anterior transverse sensory canal—Mark-Kurik 1973; Orvig 1975), implies that there was a neuromast line as in *Actinolepis* and several brachythoracids. The ventral surface of the IL is covered with tubercles, similar to those on the edges of the AVL. The tubercles on the dorsal surface are regularly arranged into four or five rows. The presence of an anterior median ventral is seen in SAM–K4649 where there is the impression of tubercles between the IL and the AVL of either side. However, the shape of this plate and the existence of a posterior median ventral cannot be demonstrated in this material.

An anterolateral (AL) has not been found associated with the ventral armour, but two specimens showing most of this plate can be referred to *Barrydalaspis* because they show ornament similar to that on the AVL. A note of caution must be introduced when associating plates by using similarities in ornament. White (1969: 303) has pointed out that in *Heightingtonaspis anglica* Traquair the ornament on the AL may differ considerably from that on the AVL. However, in the South African material there are only two types of AL present, each with ornament which matches that on one or the other of the two types of ventral armour. Thus, the criterion of association by ornament seems the most reasonable with the available material.

The AL is tall and relatively narrow, similar proportions being seen only among 'dolichothoracids' in the arctolepid described by Miles (1965). As usual the bone is raised to a focal point, which in this case is centrally placed, and from this four ridges run to the corners to divide the bone into quadrants. The posterodorsal corner is produced as in *Arctolepis decipiens* Woodward and, to some extent, in *Neophlyctaenius sherwoodi* (Denison). The pectoral emargination is very wide, matching that of the AVL. Tubercles are present on the dorsal, anterior and posterior quadrants but they are very sparse on the ventral quadrant.

The anterior dorsolateral (ADL) is known from two specimens, one of which (SAM–K4648) shows part of the trunk armour preserved in lateral view. This specimen can be associated with the holotype because of the similarity of ornament and the fact that there is evidence of scales on the body. Among the 'dolichothoracids' the ADL of *Barrydalaspis* resembles that of *Tiaraspis*. Both are tall and narrow and have a dorsal margin which slopes posterodorsally and have the anteroventral angle produced. This last feature is also seen in *Neophlyctaenius sherwoodi* (Denison 1950, fig. 2). The bone is divided into lateral and dorsolateral faces by a prominent ridge below which runs the lateral line canal. A small trochlear is developed on the anteromesial edge, immediately in front of where the ridge and lateral line converge. Beneath the trochlear the anterior margin is swollen to resemble an obstantic process, but

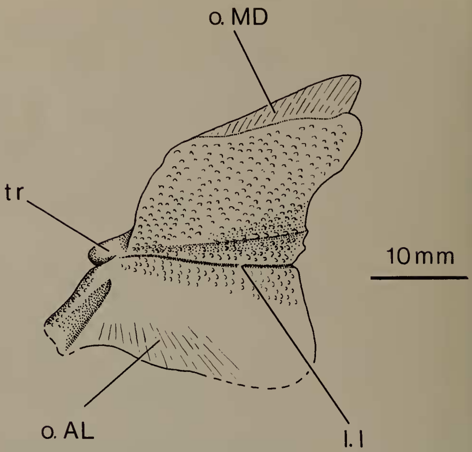

Fig. 4. *Barrydalaspis theroni* gen. et sp. nov. Restoration of anterior dorsolateral of left side. Based on SAM-K4648. l.l—lateral line, o. AL—area overlapped by anterolateral, o. MD—area overlapped by median dorsal, tr—trochlear.

it is impossible to determine if an articular face was present. The lateral face of the anteroventral corner is marked by a prominent groove. This is a feature usually found in brachythoracid arthrodires where it receives the dorsal part of the postbranchial lamina. The presence of this groove thus suggests that the dorsal part of the AL may have been inturned. The surface of the ADL is ornamented with tubercles which become larger along the posterior margin and along the crest of the ridge. The centre of radiation is found at the base of the trochlear.

One specimen (SAM-K4648) shows evidence of a posterior dorsolateral but, apart from noting the fact that it is a large plate, it is too incomplete to merit further comment. A relatively large plate is significant in showing that the lateral face of the trunk armour is not 'reduced' as it is in many brachythoracids.

The holotype and SAM-4643 show impressions of scales behind the trunk armour. The latter specimen shows that the scales are moderately large, deeper than long and completely cover at least 10 cm of the body. The scales immediately behind the posterior dorsolateral plate are deeper than those above or below and in this respect the squamation is similar to that seen in *Sigaspis* Goujet (1973, fig. 3a). There are impressions of dorsal ridge scales but no further details of these or the flank scales can be established.

Relationships of Barrydalaspis

The interrelationships of the arthrodire groups have recently been reviewed by Miles (1973) and Miles & Young (1977) and some rational outline of arthrodire phylogeny has been proposed. Within the cladistic framework provided by these authors, *Barrydalaspis* is to be regarded as a phlyctaenioid arthrodire by virtue of the possession of a 'ball and socket' dermal neck joint. Unfortunately, the relationships of *Barrydalaspis* cannot be considered further due to lack of information about the head and the median dorsal plate. The suborder Phlyctaenioidei of Miles contains the collateral infraorders Phlyctaenii and Brachythoracii. The latter can be shown to be monophyletic (Miles 1973) based on synapomorphies in features of the head and the median dorsal plate. The former, as Miles admits, is possibly a grade group. In other words monophyly has not yet been demonstrated for the Phlyctaenii (families Tiaraspidae, Groenlandaspididae, Phlyctaenaspidae, Williamaspididae and the genus *Aggeraspis*) and more rigorous analysis of the species included within the Phlyctaenii is necessary. Some recent work suggests that *Tiaraspis* and *Groenlandaspis* may be sister groups based on the synapomorphies of a high median dorsal plate and the fact that the lateral line, in crossing the posterior dorsolateral describes a sharp dorsal flexure. These two genera, plus an unnamed form from the Middle Devonian of Australia, are included in the Groenlandaspididae by Ritchie (1975).

Thus to place *Barrydalaspis* as Suborder Phlyctaenioidei incertae sedis means that it shows the synapomorphy of that Suborder but that the material does not allow us to specify its position within that group. *Barrydalaspis* resembles some members of the Brachythoracii in showing a prominent groove on the ADL to receive the AL but it is not yet clear whether this should be regarded as a synapomorphy of the brachythoracids or as a feature primitive for the Phlyctaenioidei.

'Phlyctaenaspid arthrodire'

The second type of placoderm which is recognizable in the present collection is known from ventral views of the trunk armour and a partial AL which is associated with the ventral plate because of the similarity of the ornament. This arthrodire is distinct from *Barrydalaspis* in a number of respects: the ventral armour of the trunk is much longer and narrower; the SP is set at a much lower angle (i.e. it is more nearly parallel to the sagittal plane) and lacks the medial denticles; the SP appears to be fused with the AVL throughout its length; the lateral end of the IL is swollen to produce what is here termed an 'elbow'; the ornament consists of coarse tubercles along the outer edge of the SP and IL

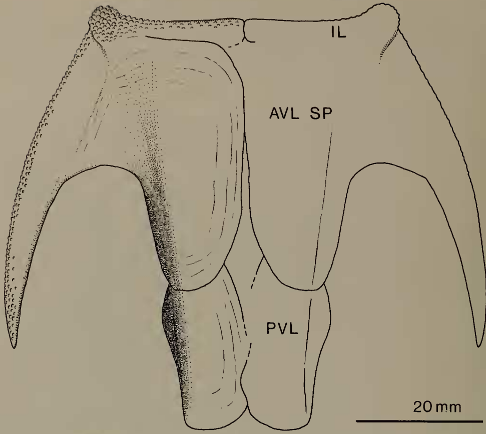

Fig. 5. 'Phlyctaenaspid arthrodire'. Restoration of ventral thoracic armour in ventral view. Based on SAM–K4640. Abbreviations as in Fig. 1.

but elsewhere is represented by minute tubercles.

The proportions and shape of the ventral armour are similar to both *Neophlyctaenius sherwoodi* (Denison 1950) and *Gaspeaspis* Pageau (1969). The former is from the late Middle or early Upper Devonian of New York State, the latter from the early Middle Devonian of Gaspé Peninsula, Quebec. As in *Gaspeaspis*, the South African form shows AVLs which meet one another in the mid-line, leaving only small areas for the anterior and posterior median ventrals (these were not seen in the South African form). The 'Ventrolateralkante' is well developed and there was probably a long postbrachial lamina. The South African phlyctaenaspid differs from both *N. sherwoodi* and *Gaspeaspis* in the relatively longer AVL and the fusion of that plate with the SP. The division between the IL and SP is recognized as a deep groove. The prominent elbow of the IL is matched elsewhere in the Lower Devonian phlyctaenaspid *Dicksonosteus* (see Goujet 1975, pl. 4 (fig. 1)). An incomplete AL (SAM–K4775) which can be referred to the ventral armour is tall with a wide pectoral emargination and a focal point which is situated ventral to the centre of the bone. Distinctively the dorsal margin slopes anteroventrally towards the front. This last feature is

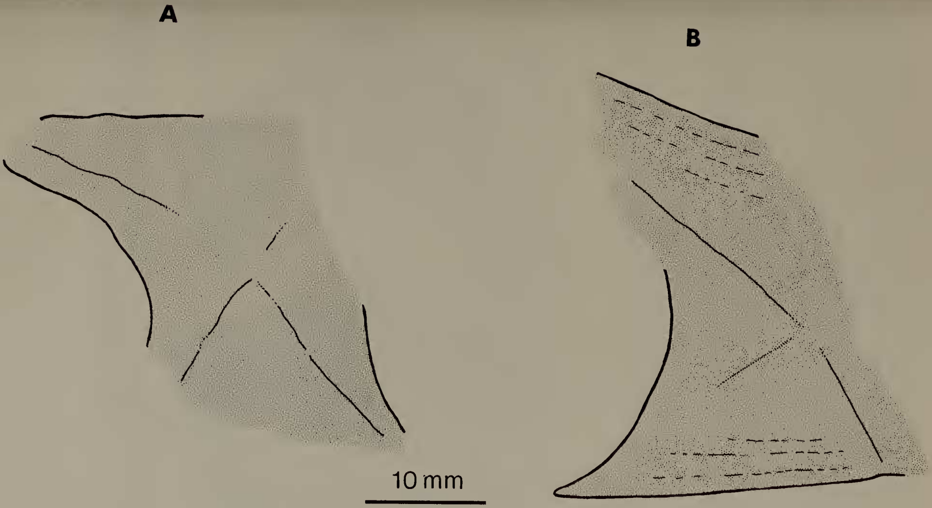

Fig. 6. A. Anterolateral plate of right side of *Barrydalaspis theroni* gen. et sp. nov. Camera lucida drawing of SAM-K4650
B. Anterolateral plate of 'phlyctaenaspid arthrodire'. Camera lucida drawing of SAM-K4775.

rare among arthrodires but is seen in species currently referred to *Phlyctaenaspis* and in *Arctolepis decipiens* (see illustrations in White 1969, figs 2–21).

In summary, this South African form is considered to be a phlyctaenaspid because it lacks the anteroventrals (a derived feature of actinolepoids (Miles & Young 1977)) and because it shows phenetic resemblances in the proportions of the ventral thoracic armour and constituent plates to certain phlyctaenaspid genera.

Arthrodire head

One specimen (SAM–K4748) shows the matrix impression of the undersurface of a partial skull roof. It cannot be associated with either of the two types described above although it is of a size that would match either. Further-

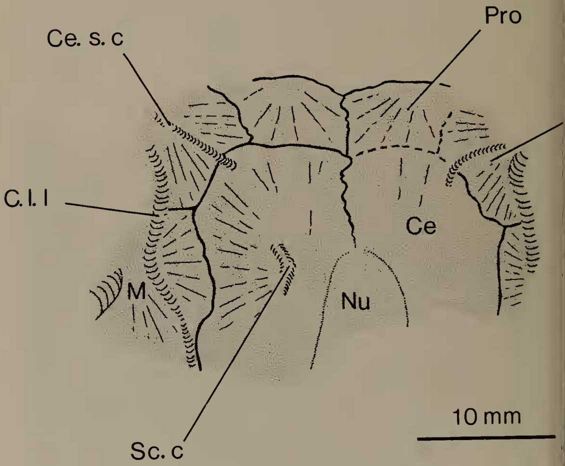

Fig. 7. Arthrodire head. Camera lucida drawing of internal cast of a partial skull roof, SAM–K4748. Ce—central, M—marginal, Nu—nuchal, Po—postorbital, Pro—preorbital, Sc.c—impression left by semicircular canals, Ce.s.c.—central sensory canal, Cl.l—cephalic division of the main lateral line.

more, it cannot be assumed that the pattern of sutures visible on the undersurface of the skull roof corresponds faithfully to that on the upper surface, which is the surface most frequently studied. For these reasons our remarks about this specimen must be limited.

The anterior end of the nuchal is narrow, gently rounded and reaches a considerable distance between the centrals. The postorbital is short and broad with the posterior margin orientated transversely. These features are seen in combination in *Gaspeaspis* (Pageau 1969, fig. 20). The marginal has a broad area of contact with the central, a feature rarely seen in actinolepoids but common in phlyctaenaspids, *Groenlandaspis* and *Aggeraspis*. What little that can be seen of the paths of the sensory canals agrees with that expected in a 'dolichothoracid'.

Undetermined arthrodire

In the collection there is one specimen (SAM–K4646, Fig. 8A) of a large arthrodire which shows coarse ornamentation unlike the forms already described

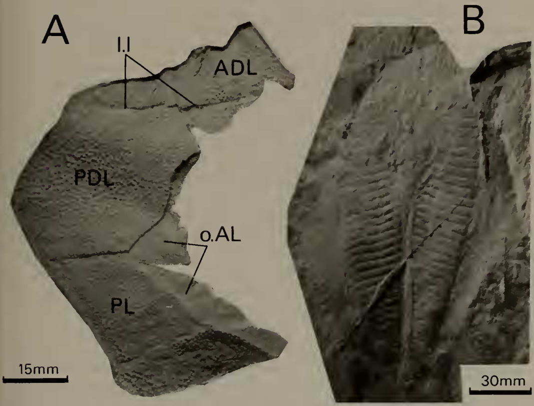

Fig. 8. A. Silicone mould of the right side of part of the trunk armour of a large arthrodire, SAM–K4646. ADL—anterior dorsolateral, PDL—posterior dorsolateral, PL—posterolateral, l.l—lateral line, o.AL—overlap area for anterolateral.
B. ?Chimaeroid egg case. Silicone mould of SAM–K4814.

from this locality. If we have interpreted this specimen correctly, this represents an impression of the posterior part of the flank of trunk armour displaying parts of the anterior dorsolateral, posterior dorsolateral and posterolateral. The anteroventral margin of the ADL and the anterior margin of the PL are similar to those in *Groenlandaspis antarcticus* Ritchie (1975). Gavin Young (pers. comm.) suggests that the size and pattern of ornament shown in this specimen is similar to the ornamentation seen in the Antarctic *Groenlandaspis.* However, it is to be admitted that similarity in ornament is a weak basis for associating this single South African specimen with the Antarctic *Groenlandaspis* and in consequence this specimen is left unnamed.

?CHIMAEROID

There is, in the collection, a specimen of an egg capsule (Fig. 8B), 160 mm in length and with approximately thirty-two unbranched narrow transverse ridges in each lateral flange.

The egg capsules of living chimaeroids are leathery, bilaterally symmetrical and elliptical in outline. They possess a membranous lateral web, which may be strengthened by simple or branched, rib-like thickenings and the margin of which can be fimbriate or entire.

Presumably by analogy with these Recent types, some eleven fossil chimaeroid eggs have been described. The earliest descriptions are of forms from the Middle Jurassic of Germany (Bessels 1869; Jaekel 1901) while the majority of later finds have been those from the Upper Cretaceous (Gill 1905; Dean 1909; Brown 1946; Voronets 1952; Vakhrameev & Pushcharovskii 1954; Obruchev 1967). Additional material has been described from the Jurassic of Canada (Warren 1947) and the Oligocene of the U.S.A. (Brown 1946). A rather differently shaped form, almost butterfly-like, has been recorded from the Triassic of Connecticut (Bock 1949) but this is possibly a pteropod.

Thus the find reported here takes the known occurrence of these supposed egg capsules back into the Devonian. In this respect it is interesting to note that the Chimaeroidei extend back only to the Jurassic (Toarcian) although members of the Menaspoidei first occur in the Upper Devonian (Patterson 1967). If, however, pelvic claspers are a primitive feature of the elasmobranchiomorphs, as is suggested by their presence in ptyctodonts, then it is reasonable to assume that placoderms also produced egg cases (Patterson 1965) and that the egg case reported above may be that of a placoderm.

ACANTHODIAN

A specimen of an incomplete pectoral spine of *Gyracanthides* (Fig. 9) is present in the collection. The spine is flattened and is deeply grooved along the medial edge of the posterior half. The upper and lower surfaces are marked with tuberculated ribs which pass obliquely across the surface and meet in a chevron pattern along the free edge. A prominent ridge runs the length of this free edge.

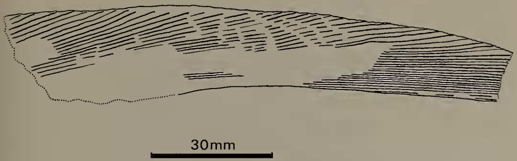

Fig. 9. *Gyracanthides* sp. Pectoral spine. Freehand sketch of rubber latex cast.

Gyracanthides is known by two species, *G. murrayi* (Woodward 1906), from the Mansfield Slate of Victoria, Australia, and *G. warreni* White (1968) from the Aztec Siltstone of Victoria Land, Antarctica. The latter is known only from two specimens representing part of the base of a pectoral spine, perhaps of the same individual (White 1968).

The South African *Gyracanthides* is similar to *G. warreni* in a number of biometric details. In both, the ribs and alternating grooves are of equal width; the ribs are almost straight; there are nine to ten ribs per cm at the base of the insertion area and thirteen to fifteen just behind this level (these counts are taken by placing a cm scale at 90° to the direction of ribbing) and the tubercles on the ribs are very closely packed. Thus, the South African *Gyracanthides* and *G. warreni* are similar in all features in which the two can be compared and there is every reason to regard them as being conspecific. *Gyracanthides murrayi* differs from *G. warreni* in that the pectoral spine and the ribs are more strongly curved and the ribs are spaced further apart, as are the tubercles upon the ribs.

THE PLANT REMAINS

The plants associated with the fish fauna consist of various types of lycopods, preserved either as 'external moulds' ('impressions'), or in some cases as matrix infillings of the cortical cavity within the stem ('endocortical casts'). Before describing the fossils, this form of preservation must be briefly reviewed.

Available for study were a number of latex casts prepared from moulds in the original matrix in South Africa, and sent to London. There was also a rather smaller number of specimens on the rock matrix, where this had been sent to London for study of the associated fish. From these, additional casts were made in latex or silicone rubber.

The lycopods represented evidently had a relatively tough cortical cylinder (Fig. 10A) within which (by analogy with Palaeozoic lycopods preserved uncompressed, as petrifications) a small stele (circle in that figure) was surrounded by a broader middle cortical cavity. As the fragmented stems became buried in matrix, this cavity became filled with mud (with or without the stelar woody cylinder at the centre).

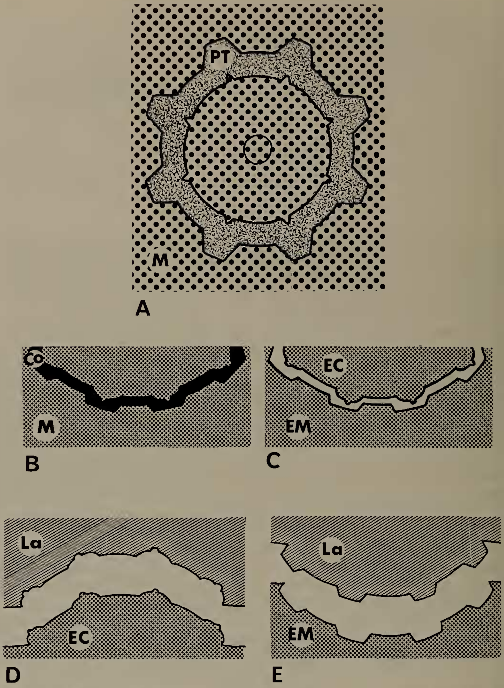

Fig. 10. Compression of stem of a lycopod such as *Archaeosigillaria*, producing the two types of fossil, endocortical cast (EC) and the external mould (EM). A. Stem lying horizontally in matrix (M). Matrix both surrounds it and fills the cortical cavity. The stem outer surface shows protruding leaf cushions; the only features on the cortical inner surface are indentations corresponding to the position of the passage of a vascular trace into the cortex. The positions of these indentations will correspond to the position of the leaf cushion. B. Compressed matrix (M) and coaly matter of the plant (Co). (The lower half only is shown.) On the outer surface protrusion of the leaf cushions is reduced with little distortion of their horizontal dimensions. The greater compressibility of plant tissue as against matrix caused collapse of

On compression, with resulting collapse of the plant tissue, the matrix filling the cortical cavity became compressed to a rod of matrix of ellipsoidal cross-section (Fig. 10B). In all cases studied, the plant material was missing, being represented either by a gap (white region in Fig. 10C), or by a dark brown (iron-rich?) porous mineral substance. The surface of an endocortical cast (EC in Fig. 10C) of such a fossil is revealed by a fracture plane passing between the cast and the enclosing matrix, i.e. the external mould. It generally shows (Fig. 14E) a topography dependent partly on any indentations on the inner surface of the cortex (e.g. passage of leaf trace, etc.) and partly on the collapse of the plant material on compression into features (e.g. leaf cushions) on the stem outer surface. Endocortical casts in this material typically show several series of longitudinal rows of bosses (Figs 12E, 14E) which correspond to the positions of leaf cushions on the original stem outer surface. They may show a small central protrusion which was a depression on the inner face of the cortex (EC in Fig. 10C). Latex 'moulds' were prepared (La in Fig. 10D) from such endocortical casts. It must be emphasized that the topography of these endocortical casts corresponds only in the broadest way to the original external appearance of the stem.

The external mould (or impression in the matrix) of the original outer surface shows a closer approximation to the original appearance of the stem. External features (e.g. leaf cushions, represented symbolically by ridges in Fig. 10A) appear in somewhat reduced topography, on such an external mould (EM in Fig. 10E). Latex casts (La in Fig. 10E), approximating to the original outer surface of the plant, may be prepared from such a mould (e.g. Fig. 13A–B).

Where leaves were still attached to such a stem, evidence of their presence is normally seen on an external mould. Where a leaf has a broad expanded base (leaf cushion) the leaf plus cushion became compressed on the upper and lower surfaces of the cylindrical stem. Such a leaf is shown in Figure 11A as though lying on the lower surface of a stem. On compression and subsequent removal (by weathering or diagenesis) of the plant material the leaf cushion is represented in the external mould by a depression in the matrix (Fig. 11C). At the bottom of this depression a narrow slit extends into the rock matrix representing the site of the lamina of the leaf. When latex is poured on to such a mould, the shape and topography of the leaf cushion are shown faithfully, but usually the latex (La in Fig. 11D), does not penetrate into the narrow mould of the

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the matrix filling the endocortical cavity into the area behind the leaf cushions. The matrix forming the endocortical cast now also shows raised bosses, corresponding to the positions of leaf cushions. C. Subsequently some, or all, of the coaly matter is removed leaving the two matrix surfaces, the endocortical cast (EC) and the external mould (EM). D. Upper half of the endocortical cast (EC) exposed by fracture plane passing over cast surface, together with latex mould (La) prepared from it, a negative version of the cortical cavity (a plaster cast taken from this mould will correspond to the original endocortical cast). E. Latex cast (La) of the external mould (EM), corresponding to the original (compressed) stem surface with protruding leaf cushions.

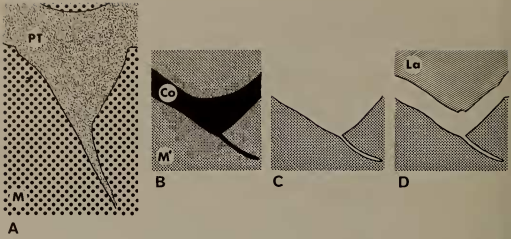

Fig. 11. *Archaeosigillaria plumsteadiae* sp. nov. Compression of leaf and leaf cushion resulting in the production, in the latex mould, of a leaf cushion showing only the 'false leaf scar'. A. Original shape of leaf and cushion (as seen in profile at edge of stem in Figs 12C, 13B), surrounded by uncompressed matrix (M) which also fills the endocortical cavity; the leaf lies in the matrix as on the lower surface of a horizontal stem. PT—plant tissue. B. Compression distorts the shape of both leaf base and leaf. The leaf cushion becomes less protruding, the thickness of the leaf lamina is reduced and its angle of emergence is decreased. Co—coaly matter. C. Removal of coaly matter (by subsequent diagenesis or weathering) gives a negative impression of the leaf cushion with a narrow mould of the leaf lamina going down into the matrix. D. Latex (La) applied to this negative mould fails to penetrate the narrow mould of the leaf lamina, leaving a 'false leaf scar' on the (positive) cast of the leaf cushion (Fig. 13A–B, f.l.s. in Fig. 12D).

leaf itself. As a result, the leaf cushion, seen (as a protruding 'positive' feature) on the latex cast prepared from this mould, does not show the leaf but merely a transverse marking—a kind of 'false leaf scar'—in the middle of the cushion (f.l.s. in Fig. 12D) where the latex failed to flow into the narrow space representing the leaf. In such a specimen the leaf may be seen in profile at one or both margins of the compressed stem (Fig. 12C; see left side of Fig. 13B).

In one specimen of *Archaeosigillaria* cf. *picosensis* the narrow mould of the leaf itself was wide enough to allow latex to enter, so producing a somewhat flattened replica of the original leaves attached to the leaf cushion surface (Figs 12A–B, 14A, F).

Although, in what is said above, the distinction is made between an endocortical cast and the external mould, the former may be encountered lying, in effect, within the latter (Fig. 14B). In this case, the visible surface features are those of the endocortical cast, but the leaves may be seen in profile at the margin (Fig. 14C–D). Unfortunately, there were no cases of 'part-and-counterpart' specimens, where external mould and endocortical cast could be seen on opposed, fractured, faces of matrix.

Two well-defined taxa of lycopods may be recognized in this material;

one is made the basis of a new species and the other is compared with a South American species. Two further kinds of rather less satisfactory lycopod fossils are also described.

Division TRACHEOPHYTA
Class LYCOPSIDA

Order PROTOLEPIDODENDRALES
Family **Archaeosigillariaceae**
Genus *Archaeosigillaria* Kidston

Archaeosigillaria plumsteadiae sp. nov.
(Figs 12C–D, 13A–B)

Etymology

Named after Dr Edna Plumstead who has contributed so much to our knowledge of South African Palaeozoic plants.

Holotype

185B, external mould (Fig. 13A).

Paratypes

161, 190A, 192A, 175. Silicone and rubber casts from the type material, two natural external moulds, are shown in Figure 13A–B.

Diagnosis

Fragments of lycopod leafy stems up to 1,5 cm diameter and 11 cm in length, represented by external moulds. Stem surface completely covered by hexagonal cushions, each typically 6,5 mm wide by 4 mm high, upper and lower edges of leaf cushions flat and in contact with cushions above and below. Cushions arranged in vertical ranks with corresponding orthostichies in alternating series. Leaves seen only in profile at margin of flattened stem mould; free part of leaf typically 6 mm long, leaving stem at about 45° and diverging from it, the apical part of the leaf being almost perpendicular to the stem. Shape of lamina otherwise unknown, but evidently not thicker than 1 mm. No evidence of leaf abscission nor of ligule or ligule pit.

Remarks

As indicated above, the shape of the leaf lamina may be seen in profile at the edges of the compressed stem (Fig. 13A, left-hand side) but over the stem surface the leaves (represented by cavities in the matrix of the fossil) cannot be seen (Fig. 11D). The latex poured into this natural mould evidently failed to flow into these cavities. Thus the only clear feature on each hexagonal leaf cushion is a transverse line at the widest part of the cushion (f.l.s. in Fig. 12D). This is rather comparable to the 'false leaf scar' of a lycopod compression fossil when a fracture plane has detached the leaf in the counterpart fossil (cf. Chaloner & Boureau 1967: 533). It must be borne in mind that whatever is seen of the leaf lamina in profile at the flattened stem margin (Figs 12C, 13B) is only a minimum length. It may actually have been longer, depending on the shape and taper of the leaf (cf. Lacey 1962, fig. 12A, D). There is no evidence of

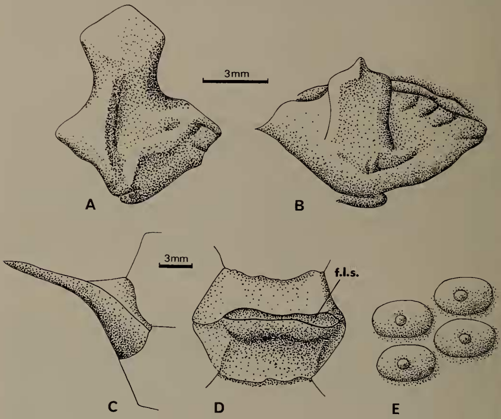

Fig. 12. *Archaeosigillaria* and 'lycopod endocortical cast.
A–D. Leaves and leaf bases of both species of *Archaeosigillaria.* Drawn from photographs of the latex cast. A–B. *Archaeosigillaria* sp. cf. *A. picosensis* Kräusel & Dolianiti. A. Rhomboidal leaf cushion with leaf attached, 2 mm long, probably complete, lying parallel to the stem surface, with its sides tapering abruptly to form a spatulate tip; SAM–K4785. B. Another leaf cushion, with a small tab-like and probably incomplete leaf emerging from the centre of the leaf cushion; SAM–K4785. C–D. *Archaeosigillaria plumsteadiae* sp. nov. C. Leaf seen in profile at side of stem, showing uncompressed dimensions of leaf cushion, and thickness of leaf lamina (as in Fig. 11A). Leaf emerging at 45° and diverging from the stem to become nearly perpendicular to it; 190A. D. Leaf cushion of holotype (as in Fig. 13A). Hexagonal, strongly protruding leaf cushion, featureless apart from the false leaf scar (f.l.s.), a transverse line at the widest part of the cushion; 185B.
E. 'Lycopod endocortical cast' with bosses on the surface produced by processes of compression and collapse explained in Figure 10. The bulge in the centre of each boss is interpreted as a feature produced by the site of passage of the leaf trace into the cortex.

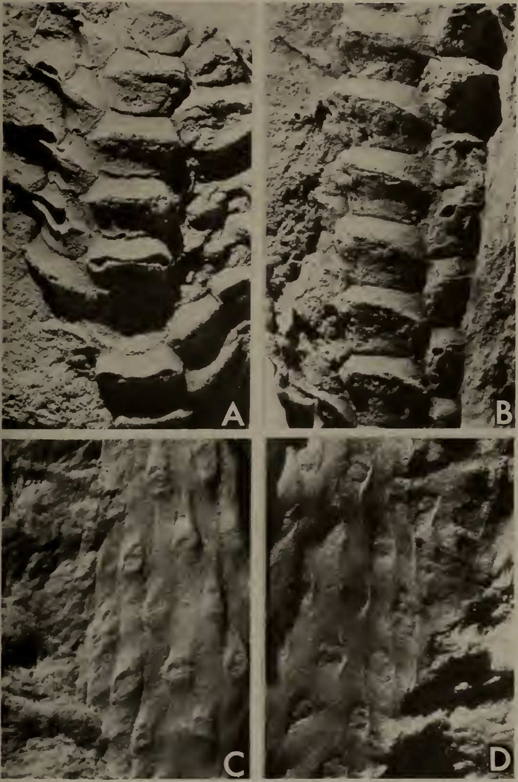

Fig. 13. A–B. *Archaeosigillaria plumsteadiae* sp. nov. Latex casts coated with ammonium chloride and illuminated from top left. A. Holotype, 185B. Stem showing three rows of contiguous hexagonal leaf cushions. × 3. B. Paratype, 161. × 3. Both specimens showing leaves in profile on the left.

C–D. Lycopod ?endocortical cast, cf. *Haplostigma irregulare* Seward. Illuminated from top left. SAM–K4744. C. Plaster cast prepared from latex mould, representing the original rock surface, showing circular raised features corresponding to positions of leaf bases. × 3. D. Latex mould showing positions of leaf bases as depressions. × 3.

leaf shedding (abscission) in these specimens; none shows a leaf scar, and hence no parichnos or vascular scar could have been represented. There is no evidence of a ligule. One specimen shows several missing leaf bases (Fig. 13A, bottom and right of specimen). The most probable explanation of this is that secondary growth of the cortex caused eventual sloughing off of the whole leaf cushions, as in the case of *Sigillaria* (Chaloner & Collinson 1975).

Grierson & Banks (1963), in their emended generic diagnosis of *Archaeosigillaria* (which the authors generally follow), do not regard this genus as having leaf cushions, and refer only to 'enlarged leaf bases becoming hexagonal on larger stems'. Their figure of the leaf of *A. vanuxemi* in profile (their pl. 35 (fig. 4)) conforms closely with that seen in our specimens. They further state (Grierson & Banks 1963: 239) that the leaves of their plant 'were persistent and that the six-sided leaf bases cannot be regarded as true cushions from which the leaf abscissed but rather as merely the enlarged base of the leaf'. The authors prefer to follow the broader concept of a leaf cushion developed by Meyen (1976) and regard the swollen leaf bases of their plant as constituting cushions even though the leaf was not abscissed, and would emphasize that they differ from Grierson & Banks only in terminology, and not in interpretation of their plant.

The broad leaf cushions of the present species with flat upper and lower faces in contact with cushions above and below are reminiscent of some Upper Carboniferous *Sigillaria* species, particularly those of the *Favularia* group (e.g. *S. elegans* Brongniart, particularly the specimens figured as *S. hexagona* Brongniart, a synonym of the former species). However, of course, *Archaeosigillaria plumsteadiae* differs from all *Sigillaria* species in having no indication of leaf abscission. The appearance of the leaf cushions and the profile view of the leaves in the present species are most closely matched in *Archaeosigillaria kidstoni* where the much smaller leafy shoots show comparable hexagonal leaf cushions (Lacey 1962, fig. 12B–C; Chaloner & Boureau 1967).

Archaeosigillaria plumsteadiae shows good general agreement with several species of *Archaeosigillaria* including *A. vanuxemi*, *A. kidstoni*, and with the Ghanaian *A. essiponensis* (Mensah & Chaloner 1971). It is noteworthy that these are all Lower Carboniferous species.

Comparison with *A. caespitosa* (Schwartz) Plumstead from the Witteberg is limited, as the holotype of this species is apparently an endocortical cast (Plumstead 1967, pl. 11 (fig. 2)), and none of the specimens she assigns to that species shows details of leaf shape. *A. plumsteadiae* differs from all other species of the genus with hexagonal leaf cushions in their being broader than long. It must be accepted that this distinction is relatively trivial, but on available information this separates the present species consistently from earlier described ones. The authors endorse Meyen's (1976) emphasis on the need for as wide a range of specimens as possible in order to establish the extent and variability in fragments of lycopod stems. Unfortunately, as here, such a range is not always available.

Archaeosigillaria sp. cf. *A. picosensis* Kräusel & Dolianiti

(Figs 12A–B, 14A, F–G)

Material

SAM–K4785 (Fig. 12A, B; Fig. 14A, F), 'D' (Fig. 14G), SAM–K4650.

Description

This species is represented by several specimens showing fragments of stem outer surface, seen only as a natural mould (i.e. a negative version of the original stem surface) in the matrix. The stem surface is formed of contiguous rhomboidal to rounded-rhomboidal leaf cushions (expanded leaf bases), typically 4 mm wide by 2,5 mm high, arranged in prominent alternating vertical series. Arrangement of the cushions must have been either in alternating whorls or a very low angle spiral. The leaves were still in attachment, the free portion being about 1 mm wide and 2 mm long.

Remarks

No leaves are seen in profile at the edges of the specimens as in the last species, perhaps because they represent fragments of a larger stem rather than parts of a complete cylinder. However, latex evidently penetrated the leaf cavities in the mould more freely than in *A. plumsteadiae* (possibly due to greater thickness of the leaves) so that something of the form of the leaves is seen in the latex cast of the stem prepared from the mould (Figs 12A–B, 14A, F). This can be compared with the situation in *A. conferta* (Menendez 1965) where leaves are seen on the surface because the fracture plane exposing the fossil followed the plane of the leaf laminae rather than the stem surface. It is possible that these small tab-like leaves (seen in the latex casts) represent incomplete infill by the latex of a larger leaf cavity, or possibly the original leaf shape was somewhat eroded before fossilization. It is interesting to compare the situation here with that in *A. plumsteadiae*, where the latex did not penetrate the leaf cavity. On one of the specimens (Fig. 14G) there is evidence of secondary cortical growth resulting in the lateral separation of the leaf bases revealing (?) cortical tissue between them. This is, of course, a common phenomenon in many *Lepidodendron* species (Thomas 1966).

In the leaf shape and arrangement this material agrees well with those species of *Archaeosigillaria* seen to have short tab-like leaves turning abruptly from the leaf cushion to parallel the stem surface or lie obliquely to it; these include *A. vanuxemi*, *A. kidstoni*, and *A. essiponensis*, with leaves showing at the side of the stem, and more particularly *A. picosensis*. This plant, from the Picos member in Brazil (Lower Devonian according to Kräusel & Dolianiti 1957), is preserved like the specimens here as a natural mould with leaves showing on the surface and is the closest species to the Bokkeveld plant. Those authors describe their specimen (free translation from the German summary) as 'small stems, [covered with] leaf cushions pressed together, rounded-angular to rhomboidal, also in part hexagonal, bearing in their upper part a small thin leaf' (literally, leaflet). It should be noted that the age of Kräusel & Dolianiti's specimen, cited by them as Lower Devonian, may well be much younger. Sampaio & Northfleet (1973) offer an age correlation for the Picos member (of the Pimenteiras Formation) as ranging between Emsian and Eifelian; Bär & Riegel (1974) favour 'Middle Devonian Age'. The age of *A. picosensis* is probably best placed only within a broad bracket between Emsian and Frasnian (Brito 1971, fig. 10).

LYCOPOD ENDOCORTICAL CASTS

(Fig. 14B–E)

Material

SAM–K4790, K4798*a*.

Remarks

The specimen illustrated in Figure 14E is one of several in the latex casts available in which the topography of the fossil appears to represent only a very blurred version of the lycopod stem. This cannot be reconciled with leaf bases or remains of attached leaves, and this fossil is interpreted as representing an endocortical cast. This shows the positions of leaves in the form of bulges or bosses on the endocortical cast, which simulate leaf bases or cushions (EC in Figs 10C–D, 12E, 14E). One of these casts K4798*a* (Fig. 14B–D), besides showing these vertically seriated bosses, also shows leaves in profile along the margin. The leaves appear to be preserved in a brown mineral substance which must have come to occupy the site of the original plant tissue. This mineral matter is a thin layer on the outside of the cast, representing the cortical tissue and leaf bases of the stem. The leaves are somewhat similar to those of some species of *Archaeosigillaria*, such as *A. essiponensis* (Mensah & Chaloner 1971) and *A. kidstoni* (Lacey 1962; Chaloner & Boureau 1967), being short with a broad base and tapering towards the apex.

On the other cast SAM–K4790 (Fig. 14E) this mineral matter is not present, and on the left-hand side a cavity can be seen representing the gap between the endocortical cast and the external mould, i.e. the site of cortical

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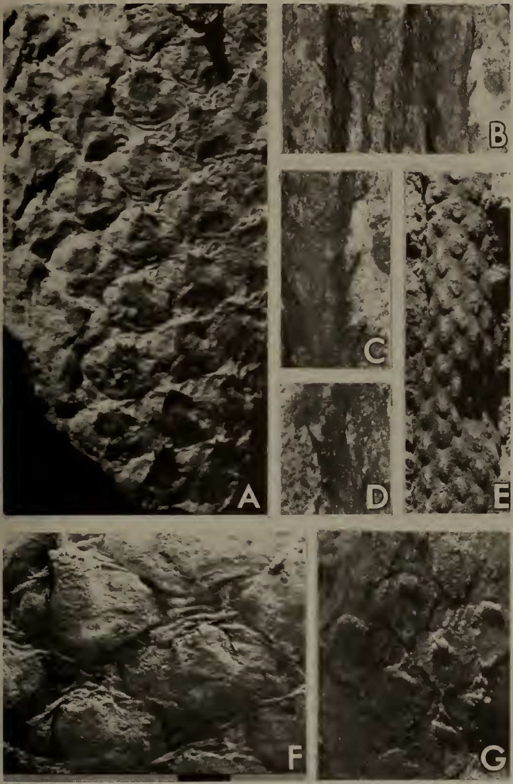
Fig. 14. A, F, G. *Archaeosigillaria* sp. cf. *A. picosensis* Kräusel and Dolianiti. A. Latex cast of a fragment of an external mould showing contiguous rhomboidal leaf bases with attached leaves, one of which, near top left, is more complete than the others; SAM–K4785. F. Scanning Electron Micrograph photograph of an area of the same specimen, taken on a Cambridge S600 at a stub angle of 10°. (Horizontal axis only, × 12.) G. Latex cast showing separation of leaf bases, SAM 'D' × 7,5.

B–E. Indeterminable lycopod endocortical casts. Photographs of original rock surface. B. Part of cast immersed in alcohol, photographed to show vertical files of raised bosses on the surface. At both sides there is a thin layer of mineral matter, representing the site of original plant tissue, and showing leaves in profile, one on the left-hand edge, three on the right. SAM–K4798*a*. × 3. C–D. Detail of leaves (immersed in alcohol). Short leaves with a broad base tapering to a thin lamina, at about 45° to the stem surface. × 5.

E. Cast photographed dry, lighting from top left, showing seriated raised bosses; SAM–K4790. × 3.


A
B
C
D
E
F
G

tissue. These endocortical casts are generally comparable to those formed on the matrix infill inside *A. essiponensis* (cf. Plumstead 1967, pl. 11 (fig. 2); Mensah & Chaloner 1971, pl. 64 (fig. 7)), but other genera can produce similar casts (e.g. Plumstead 1967, pl. 15 (fig. 3) attributed to *Haplostigma*). The authors do not believe that such fossils can be assigned to genera based on characteristics of leaf cushion shape and prefer to leave these present specimens unassigned.

Lycopod ?endocortical cast, cf. *Haplostigma irregulare* Seward

(Fig. 13C–D)

Description

The specimen figured in Figure 13D (and a plaster cast prepared from that latex mould, so representing the original rock surface, Fig. 13C) shows vertically seriated round markings on a grooved stem surface, the grooves apparently separating elongated leaf cushions. This specimen is preserved as a 'positive' cast apparently showing detail of the surface topography, rather than the blurred bosses described above. It is believed that this is due to the plant possessing only a narrow zone of cortical tissue, which in compression would collapse to a uniformly thin layer more or less conforming to the stem's original external topography on both surfaces. No leaves are in evidence in the material, and it is not clear whether they were abscissed. It is accordingly regarded as generically indeterminable but is figured since it shows some resemblance to the holotype of *Haplostigma irregulare* Seward, 1903, from the Bokkeveld (as refigured by Plumstead 1967, pl. 13 (fig. 3), pl. 14 (fig. 5)). It is also comparable to the specimens attributed to the same species by Kräusel (1960, fig. 88) from the Ponta Grossa Formation of Brazil.

DISCUSSION

The Bokkeveld Series consists of alternating bands of sandstone and shale which vary in number and thickness over wide areas of the Cape Province (Plumstead 1967). This is overlain conformably by the Witteberg Series. Most authors divide the Bokkeveld Series into lower and upper beds which, by reason of the contained fossils, are thought to represent marine and shallow marine/freshwater deposits respectively. One author, Swart (1950), suggests that in at least one locality shallow marine conditions persisted throughout the Bokkeveld Series. In the Barrydale area the more usual freshwater beds are clearly seen, and the fish are found in these upper beds of the Series.

The interpretation of the lower beds as representing marine conditions is well founded. A large number of marine species have been described (Lake 1904; Reed 1925 and refs; Haughton 1969) including lamellibranchs, brachiopods, trilobites, gastropods, cephalopods, corals and crinoids. A consensus of opinion holds that the lower marine beds of the Bokkeveld Series are of Lower Devonian age, and Boucot *et al.* (1967) are more precise in suggesting an Emsian age.

Further, several authors (Du Toit 1939; Doumani 1965; Haughton 1969) note the close similarity of the marine faunas of the Bokkeveld with the presumed contemporaneous strata in the Falkland Islands, Bolivia, Argentina, southern Brazil and Antarctica. Therefore, on the strength of the evidence of the underlying marine sequence, the fish- and plant-bearing beds of the Bokkeveld Series cannot be older than Middle Devonian.

The only information available here (J. N. Theron, pers. comm.) on the position of the fish fauna is that it is some '6 000 ft' below the fish zone of the Upper Witteberg (Gardiner 1969) and as such may be anything from Middle Devonian to Lower Carboniferous. At first sight the fact that the fauna contains two dolichothoracid arthrodires suggests a Lower/Middle Devonian age since the dolichothoracids reached their acme in the Emsian/Eifelian (Miles 1969). Nevertheless, *Groenlandaspis* is a widespread late Devonian representative of the dolichothoracids, while *Neophlyctaenius* survived into the Frasnian in the eastern United States (Denison 1950). Since one of the dolichothoracids is a completely new form and the other closely resembles *Phlyctaenius*, their stratigraphic significance is not apparent. Similarly, the occurrence of large arthrodire plates resembling *Groenlandaspis* does no more than confirm a Middle or Upper Devonian age. However, from the same general area as the other specimens, but not, unfortunately, as accurately located within the sequence, occurs a spine of the large acanthodian *Gyracanthides*. Elsewhere *Gyracanthides* is recorded from the Upper Devonian of Victorialand, Antarctica (White 1968) and the Lower Carboniferous of Mansfield, Australia (Woodward 1906).

The Upper Devonian Antarctic fish fauna from Victorialand is characterized by the presence of *Bothriolepis*, *Phyllolepis*, *Groenlandaspis*, holoptychiids and various acanthodians and sharks (Gavin Young pers. comm.) whereas the Australian Lower Carboniferous fauna from Mansfield has *Strepsodus*, *Ctenodus*, *Elonichthys* and three acanthodian genera but no placoderm genera. There can be little doubt that the Antarctic fauna is Upper Devonian (Young 1974) and if this South African fauna is to be interpreted as being of similar age then the absence of more typical Upper Devonian forms such as *Bothriolepis*, *Phyllolepis* and *Holoptychius* from the Bokkeveld is difficult to understand. Nevertheless the presence of a typical Lower Carboniferous fish fauna in the overlying Witteberg Series, some 1 800 m (6 000 ft) above the fish-bearing layer of the Bokkeveld convinces the authors that the fauna under discussion must be at least of Upper Devonian age and the only safe conclusion that can be drawn is that the fish fauna is Middle/Upper Devonian.

The only plants in this flora which may be of significance in dating these rocks are the two species of *Archaeosigillaria*, and in particular the very distinctive *A. plumsteadiae*. Plants belonging to this genus range from Middle Devonian to Upper Carboniferous (Banks 1960; Grierson & Banks 1963; Lejal 1970; Mensah & Chaloner 1971). Recently Lejal-Nicol (1975) has described a number of typically Middle or Upper Devonian and Lower Carboniferous lycopod genera (including *Protolepidodendron*, *Lepidodendropsis*, *Lepidosigillaria* and *Archaeosigillaria*) from Libya. Lejal-Nicol maintains that these deposits are of Lower Devonian age, and a further flora is described containing *A. kidstoni* from rocks believed to be of Pre-Siegenian age (either Gedinnian or Siluro-Devonian). These genera, which are characterized by various peculiarities of their leaf cushion shape and arrangement, do not appear in Europe and North America until the Middle or Upper Devonian (Grierson & Banks 1963; Chaloner & Boureau 1967). Typical lycopods of the Lower Devonian from continents other than Africa (e.g. *Drepanophycus* and *Baragwanathia*) show no significant development of leaf base expansion comparable to the cushions of the later arborescent lycopods. Even in the Middle Devonian lycopods with a leaf cushion or cushion-like feature (e.g. *Protolepidodendron*, *Leclercqia*, and *Colpodexylon*) this feature is poorly developed compared with that seen in the arborescent lycopods of the late Devonian and early Carboniferous. On this basis an extreme age bracket is put on these Bokkeveld lycopods as Middle Devonian to Lower Carboniferous, with the strongest possibility of their being Upper Devonian (Frasnian–Fammenian).

It may be useful to note that shoots of lycopods such as *Archaeosigillaria* were evidently among the more robust of plant remains occurring in the Upper Palaeozoic; they commonly survived when no, or few, other plants were represented in coarse non-marine lithologies, or even in marine environments. *Archaeosigillaria kidstoni* occurs in the coral/brachiopod-rich Carboniferous Limestone in Britain (Chaloner & Boureau 1967) and the holotype of *A. vanuxemi* is closely associated with a brachiopod fauna. The present association of lycopods with fish remains is therefore not surprising.

The evidence of both the fish and the plants suggests, therefore, that these fossils come from an horizon within the Bokkeveld Series that is either Middle or Upper Devonian. Hopefully, further collecting in these strata will yield fossils giving a more precise stratigraphic position.

ACKNOWLEDGEMENTS

We should like to thank Dr J. N. Theron for bringing this material to our attention. Our thanks are also due to Drs R. S. Miles and G. C. Young for comments on the fishes, and to Dr O. Rösler and Professors H. P. Banks and J. D. Grierson for comments on South American stratigraphy and the lycopods. Finally, we thank the authorities of the South African Museum for allowing us to comment on this material.

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ADDENDUM ADDED IN PRESS

After preparing this manuscript for publication, the authors received (August 1979) an offprint of Plumstead's (1977) account of *Zosterophyllum de-vriesii* and *Z. bokkeveldensis.* (The former name is here hyphenated to give a single epithet, in accordance with the International Code of Botanical Nomenclature, Art. 23.) It is immediately evident from Plumstead's figures and specimen citations that the species described above as *Archaeosigillaria plumsteadiae* is based on the same fossil assemblage (and in part the same specimens?), from the same locality, as her *Zosterophyllum de-vriesii.* No basis in her paper is found for revising the views expressed here, that these cylindrical structures covered with closely spaced hexagonal leaf cushions represent a lycopod vegetative axis and not a zosterophyll fructification. Her photographs and her text-figure 3 (central figure) clearly show what has been here interpreted as the free tips of the leaves, seen in profile at the stem margin (her 'bisected empty sporangial sacs'). The clear validity and priority of Plumstead's specific name is acknowledged, and accordingly it is reassigned:

Archaeosigillaria de-vriesii (Plumstead) comb. nov.

Synonyms:

Zosterophyllum de vriesii Plumstead, 1977: 270, text-fig. 3, pl. 1 (figs 1–10).

Archaeosigillaria plumsteadiae Chaloner *et al.* 1979 (this paper): figs 12C–D, 13A–B.

Plumstead's *Zosterophyllum bokkeveldensis* does not appear to be strikingly distinct from *Z. de-vriesii,* but her view that they are distinct species is not challenged. It is agreed that they are congeneric (i.e. may both be placed in *Archaeosigillaria*), but no formal reassignment of the former species is suggested.

The age implication of the authors' systematic assignment of these plant fossils is, of course, at variance with Plumstead's. In rejecting assignment to *Zosterophyllum,* the suggestion of a Middle or Upper Devonian horizon rather than the Lower Devonian which was implicit in attributing these fossils to *Zosterophyllum,* is sustained.

REFERENCE

Plumstead, E. P. 1977. A new Phytostratigraphical Devonian Zone in southern Africa which includes the first record of *Zosterophyllum. Trans. geol. Soc. S. Afr.* **80**: 267–277.

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